Immigration and extirpation selectivity patterns of brachiopods and bivalves across a Carboniferous glacial to non-glacial transition (Pennsylvanian, central western Argentina) and their influence in building the biotic bathymetric gradient

Balseiro D.[a,b,*], Halpern K.[c]

[a] Universidad Nacional de Córdoba, Facultad de Ciencias Exactas Físicas y Naturales, Avenida Vélez Sarsfield 1611 Ciudad Universitaria, X5016GCA Córdoba, Argentina
[b] CONICET, Centro de Investigaciones en Ciencias de la Tierra (CICTERRA), Córdoba, Argentina
[c] Instituto de Geología de Costas y del Cuaternario (IGCyC-CIC), CONICET, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Dean Funes 3250, B7602AYJ Mar del Plata, Argentina

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ABSTRACT

The growth and demise of glaciers during the Late Paleozoic ice age had profound consequences on the marine biota. In central western Argentina the transition from glacial to non-glacial interval during the Pennsylvanian, caused a major regional turnover which remodeled the bathymetric diversity gradient. In order to understand the nature of the environmental changes related to such turnover event, we compared selectivity patterns in extirpation and immigration of bivalves and brachiopods using logistic regression. We tested for a wide range of potential drivers of extirpation and immigration, namely body size, geographic range size, environmental breadth, preferred depth, metabolic rates, infaunalism and taxonomic identity. While extirpation preferentially hit brachiopods and genera having smaller geographic ranges and smaller body sizes, immigration was related to genera with preference for deeper environment and small geographic ranges.

Extirpation selectivity was not uniform along the bathymetric gradient. Both geographic range and body size selectivity are stronger towards deeper environments. Each clade, on the other hand, showed idiosyncratic responses to climate change. While brachiopods show extirpation selectivity for smaller geographic ranges, small sized bivalves were preferentially extirpated. These contrasting selectivity regimes, however, could be reflecting different faunal responses to the same environmental changing factor, namely higher thermal amplitude. Immigration in both brachiopods and bivalves was related to preference to deep environments, confirming previous results. However, brachiopods also showed preferential immigration of small geographic range genera, which is puzzling given the extinction selectivity related to the glacial non-glacial transition. Possible explanations point to a brief time span in which an increase in thermal amplitude occurred. The rapid climate changes, particularly related to a rise in maximum temperatures, lead the ecological response of the benthic faunas. Differences in extinction and immigration selectivity along the bathymetric gradient, suggest that the turnover event also remodeled the bathymetric gradient in body size and biogeographic structure and brachiopod:bivalve proportions. Such changes were driven by extirpation, contrasting with the remodeling of the bathymetric diversity gradient that was driven by immigration. Our results, therefore, highlight that immigration and extirpation can shape different aspects of the bathymetric biotic gradient.

1. Introduction

The Late Paleozoic Ice Age (LPIA) had multiple glacial intervals alternating with nonglacial intervals during several million-years (Fielding et al., 2008). Although both global and paleotropical regional analyses have shown that biotic responses to the LPIA were ecological and macroevolutionary stability (Powell, 2005, 2007; Bonelli and Patzkowsky, 2008, 2011; Badyrka et al., 2013), analyses in proximal regions underscore complex outcomes to the advance and retreat of glacial centers (Clapham and James, 2008, 2012; Sterren and Cisterna, 2010; Balseiro, 2016a; Balseiro and Halpern, 2016).

Facing a major glacial to nonglacial transition, occurring within the

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Carboniferous glacial peak of the LPIA (Montañez and Poulsen, 2013), brachiopod-bivalve communities in western Argentina recorded important compositional changes (Sterren and Cisterna, 2010; Balseiro, 2016a). Consequences related to such turnover included remodeling of the bathymetric diversity gradient, modification of the taxonomic structure of the regional community (Balseiro, 2016a) and niche instability of survivor genera (Balseiro and Halpern, 2016). Further analyses on potential selectivity showed that turnover was not taxonomic nor environmentally homogeneous, being harsher in brachiopods and in offshore settings (Balseiro, 2016a). Moreover, while a severe taxonomic turnover, detected in brachiopods, was caused by higher extirpation (Balseiro, 2016a), a stronger turnover in the offshore was a result of higher immigration into that environment (Balseiro and Halpern, 2016), indicating that turnover in both cases was driven by contrasting dynamics.

Further biological factors, such as body size, geographic range, life habit or depth preferences (Payne and Finnegan, 2007; Powell, 2007; Finnegan and Droser, 2008; Saupe et al., 2014; Balseiro and Halpern, 2016), that could explain the observed taxonomic or environmental selectivity have not been studied, hindering the comprehension of the ultimate causes controlling extirpation or immigration in the region during the climatic event. By using binary logistic regression (Payne and Finnegan, 2007), we can assess the association between these two processes and each ecological predictor. A further analysis of selectivity using an environmental framework helps to determine which of these factors are key in modifying the bathymetric biotic gradient. On the one hand, given that temperature is an important factor related to metabolism (Gillooly et al., 2001; Brown et al., 2004), temperature rise related to the glacial to non-glacial transition in ice proximal regions could had been related to higher extirpation rates, contrasting with distal regions where temperature was more stable during the acme of the LPIA (Montañez and Poulsen, 2013) and turnover was reduced (Badyrka et al., 2013). Metabolic rate has been recently proposed as a proxy of extinction probability (Strotz et al., 2018). Considering that brachiopods and bivalves differ in their metabolic rates (Payne et al., 2014), it could be expected that their differential survivorship (Balseiro and Halpern, 2016) was actually a consequence of selectivity based on metabolic rates. On the other hand, because cosmopolitan genera dominated the near close-by regions during the Moscovian (Badyrka et al., 2013), we would expect immigrant taxa with broad geographic ranges. In addition, body size is affected by productivity (Pyenson and Vermeij, 2016), and immigration in the region has been related to a rise in resource availability in offshore settings (Balseiro, 2016a; Balseiro and Halpern, 2016). Therefore we could predict that larger body size taxa preferentially immigrated to the region or at least to deep environments.

In this contribution we attempt to understand ecological factors related to the high taxonomic turnover observed in ice proximal regions during the LPIA (Balseiro, 2016a). For this aim we study potential extirpation and immigration selectivity related to different factors such as rarity (Harnik et al., 2012), metabolism or body size (Harnik, 2011).

2. Geological setting

Neopaleozoic marine deposits from western Argentina basins (Río Blanco, Calingasta-Uspallata and western Paganzo basin, Fig. 1) studied herein include a variety of siliciclastic rocks that date from middle to Late Carboniferous (Late Serpukovian-Bashkirian to Moscovian-Kasimovian age). These sedimentary successions evidence the climatic transition from a glacial to a non-glacial interval recognized in southwestern South America (Limarino et al., 2006; Henry et al., 2008; Gulbranson et al., 2010, 2015; López Gamundí, 2010).

Glacial and glaciomarine deposits extend regionally characterizing the lower Pennsylvanian sequences from central western Argentina (Fig. 2) and correspond to the *Levipustula levis* Biozone (Amos and Rolleri, 1965) and the *Aseptella-Tuberculatella/Rhipidomella-Micraphelia*
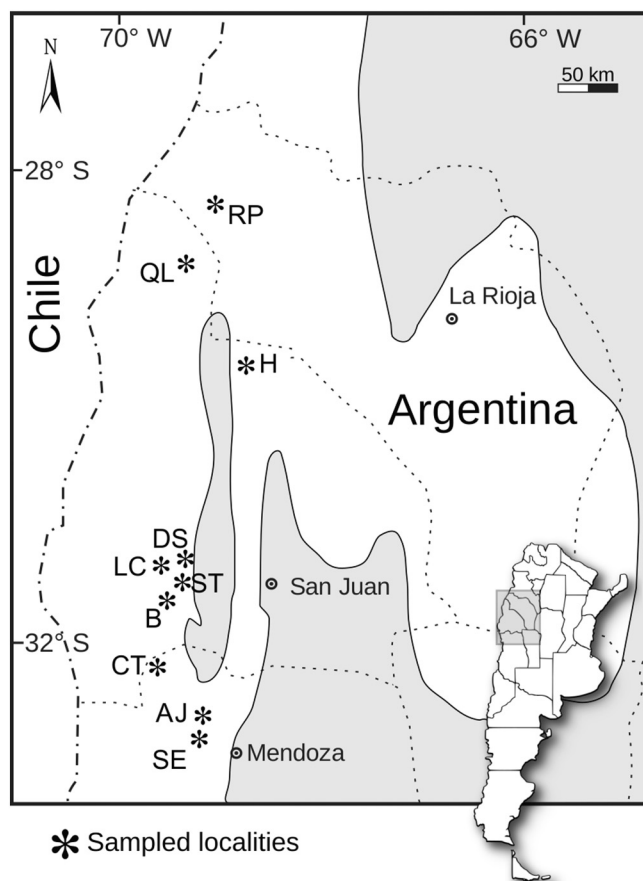

Fig. 1. Map of the study area showing basin paleogeography; positive paleo-topography in grey. Localities: RP, Río Blanco Anticlinal; QL, Quebrada Larga; H, Huaco area (Quebrada La Herradura and Quebrada La Delfina); DS, Quebrada del Salto; LC, La Capilla area (Las Cambachas and Las Juntas); ST, Sierra del Tontal. B, Barreal area (Barreal Anticlinal, Leoncito, Quebrada Majaditas, Cordón del Naranjo). CT, Cordillera del Tigre; AJ, Agua de Jagüel; SE, Quebrada Santa Elena. Modified from Balseiro (2016a).

faunas (Cisterna et al., 2017). These diverse marine invertebrate faunas, dominated by brachiopods and bivalves (Cisterna and Sterren, 2010; Sterren and Cisterna, 2010), have been identified in several stratigraphic units. Such units correspond to transgressive fine-grained sandstones and siltstones with or without ice-rafted debris in mudstones and claystones, and are interpreted as a periglacial open marine shelf environment (Limarino et al., 2006; Cisterna and Sterren, 2016).

The later Moscovian-Kasimovian records (Gulbranson et al., 2010; Césari et al., 2011)- show the development of a different marine fauna (brachiopods, gastropods, bivalves, crinoids, etc.) that characterize the *Tivertonia jachalensis-Streptorhynchus inaequiornatus* Biozone (Sabattini et al., 1990) and its faunal coevals (Cisterna, 2010, Fig. 2). Its records can be traced to the Rio Blanco and Paganzo basins (Sterren and Cisterna, 2010); and its equivalent faunas have also been mentioned for the Callingasta-Uspallata basin (Cisterna, 2010). This fauna is related to a climate amelioration suggested for the Argentinian basins towards the Late Carboniferous (González and Díaz Saravia, 2010; Sterren and Cisterna, 2010; Limarino et al., 2014; Gulbranson et al., 2015).

A pronounced lithostratigraphical change is recorded in the central western Argentine basins between both faunas (Fig. 2), containing abundant paleosoils, fluvial and fluvio-deltaic facies with several micro and macrofloral remains that ranging from the NBG zone to a transition zone with abundant ferns and conifers (Gulbranson et al., 2015).

All these sections have been thoroughly studied, including their taxonomic, taphonomic and paleoecological aspects, and its
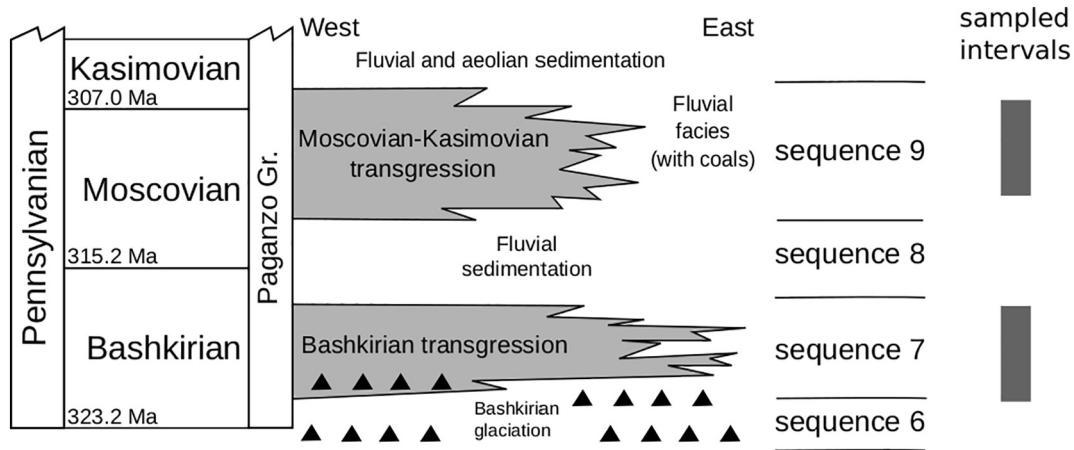
Fig. 2. Stratigraphic framework, sequence stratigraphy and chronostratigraphy of the studied area. Modified from Limarino et al. (2006), Césari et al. (2011), Gulbranson et al. (2015) and Balseiro (2016a).

biostratigraphy and sequence stratigraphy are widely known (Limarino et al., 2006; Césari et al., 2007, 2011; Gulbranson et al., 2010; López Gamundí and Buatois, 2010; Sterren and Cisterna, 2010; Cisterna et al., 2011; Cisterna and Sterren, 2016) allowing us to go further in analytical paleoecological studies.

3. Material and methods

3.1. Data

3.1.1. Occurrence data

For the current analyses we used the data set previously published by (Balseiro, 2016a) which is freely accessible at Dryad Digital Repository (Balseiro, 2016b). In brief, the data set is based on literature and consists of brachiopod and bivalve occurrences from 99 bed-level samples coming from 15 different localities (Fig. 1). 48 samples come from the Bashkirian, while 51 samples come from the Moscovian–Kasimovian. The data set totals 88 genera and 481 occurrences.

Based on sedimentological and ichnological aspects (Henry et al., 2008, 2010; Desjardins et al., 2009, 2010; Alonso-Muruaga et al., 2013; Buatois et al., 2013), all samples were assigned to one out of 3 environments, namely shallow subtidal (above fair weather wave base), deep subtidal (between fair weather wave base and storm wave base), and offshore (below storm wave base). Environmental coverage is evidently uneven within and between intervals (Fig. 3).

A detailed taphonomic analysis of much of the dataset was performed by Sterren (2008), while further taphonomic biases were tested by Balseiro et al. (2014) for the Moscovian–Kasimovian part of the data set. Neither storm reworking nor time averaging seems to have had significant consequences on the composition of samples (Balseiro et al., 2014). Biases related to sequence stratigraphy can be disregarded as sampling in both intervals is mostly restricted to the early transgressive system tracks, namely sequences 7 and 9 (see Fig. 2; Limarino et al., 2006; Desjardins et al., 2009; Alonso-Muruaga et al., 2013).
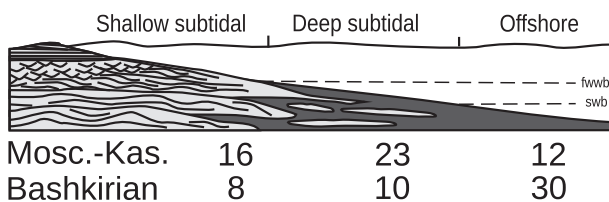

Fig. 3. Environmental sampling coverage of the studied intervals. Abbreviations: Mosk.-Kas., Moscovian-Kasimovian. Modified from Balseiro (2016a).

3.1.2. Body size data

Body size estimation was based on maximum longitudinal (x) and transverse (y) length for all specimens coming from Western Argentina figured in the literature. We used both illustrated material measured using a digital caliper, and linear measurements given by original authors when available. These linear dimensions represent the most common method of measurements of shell size, and Krause et al. (2007) have shown that these kind of data record reliable information for body size estimation.

3.2. Methods

3.2.1. Taxonomic identity

All genera were classified as brachiopods and bivalves to test for some phylogenetic signal in the selectivity for extirpation. The intensity of the phylogenetic signal can provide insight to the underlying mechanisms linked to extinction by representing the degree of non-independence of an ecological trait of a monophyletic clade. Although taxonomy does not record actual phylogenetic information, Harnik et al. (2014) and Soul and Friedman (2015) have shown that it is a useful proxy.

3.2.2. Preferred depth

We calculated preferred depth (PD) for all genera following Balseiro and Halpern (2016). Preferred depth is estimated based on,

$$PD = \Sigma\,[(occu_i/\Sigma occu_i) \times X_i]/x \tag{1}$$

where x is the number of environments (three in our case), X_i is a constant that represents water depth which has values of 0, 1.5 and 3 for the shallow subtidal, deep subtidal and offshore, respectively; while $occu_i$ is the taxon's occupancy in the ith environment.

3.2.3. Environmental breadth

Environmental breadth (EB′) of genera was estimated using the equation put forward by Hurlbert (1978) and modified for occurrences (Balseiro and Halpern, 2016),

$$EB' = (EB \times N - n_{min})/(N - n_{min}) \tag{2}$$

where

$$EB = O^2/[N \times \Sigma(o_i^2/n_i)] \tag{3}$$

O is the total number of occurrences of the taxon, o_i the number of occurrences in the ith environment, N the total number of samples, n_i the number of samples in the ith environment, and n_{min} is the minimum number of samples found in any environment.

3.2.4. Regional abundance

We used regional occupancy (Ocu) as a proxy for regional abundance. Occupancy has shown to be a good estimator of abundance both in ecological (Holt et al., 2002) and paleoecological datasets (Ivany et al., 2009). Moreover, regional occupancy is highly correlated with other measures of occupancy in our dataset (Balseiro and Halpern, 2016).

3.2.5. Body size

The geometric mean of longitudinal (x) and transverse (y) measurements was used as a proxy for body size (BZ). Geometric mean has proven to be a good proxy for more complex estimators of body size (Kosnik et al., 2006). To estimate the body size of each genus, we first calculate the maximum body size of each identified species within the genus present in the dataset (Supplementary information), and then calculated the generic body size as the mean body size of all constituent species. Calculating genera body sizes as the maximum value among all measured specimens, gave virtually identical results. Body size values were log-transformed, using base 2 logarithm, to indicate two-fold increments in body size.

3.2.6. Metabolic rate

Because brachiopods and bivalves have contrasting differences in the relationship between shell size and actual biomass, our measure of body size could not reflect differences in energetic requirements between both clades. To avoid this issue we analyzed metabolic rates (MR) of each genus following Payne et al. (2014). Basal metabolic rates are indicative of the maintenance energy requirements of organisms (Strotz et al., 2018). Metabolic rate per individual genus was calculated as (Gillooly et al., 2001),

$$MR = b_0 \times e^{E/k \times T} \times M^{3/4} \tag{4}$$

where E is activation energy (0.65 eV), k is Boltzmann's constant ($8.61733324 \times 10^{-5}$ eVK^{-1}), T is absolute temperature (in Kelvin) at which metabolism occurs and b_0 is a scaling constant that differs among mayor taxonomic groups, and M is biomass. Following Payne et al. (2014) b_0 was 6.5×10^{10} Wkg$^{-3/4}$ for rhynchonelliform brachiopods, 5.6×10^{10} Wkg$^{-3/4}$ for linguliform brachiopods, 1.4×10^{11} Wkg$^{-3/4}$ for heterodont bivalves and 1.3×10^{11} Wkg$^{-3/4}$ for non-heterodont bivalves. We set T at 277 K for the glacial stage, based on that water stratifies at 277 K (= 4 °C) when the surface is frozen, and T at 283 K for the nonglacial stage as current SST on pacific margin of South America is about 6 K higher than during the last glacial maximum. In any case, because we did not compare glacial and non-glacial metabolic rates, setting T at different values did not change our results. Finally, M was calculated based on regressions between maximum shell length (L, in millimeters) and ash free dry mass (AFDM, in gramms) (Payne et al., 2014). The equations for estimating mass are,

$$M = 8.0 \times 10^{-7} \times L^{3.34} \tag{5}$$

for brachiopods, and

$$M = 1.0 \times 10^{-5} \times L^{2.95} \tag{6}$$

for bivalves (Payne et al., 2014). Maximum shell length for each genus was calculated as the mean of maximum length of all present species (as the case of body size).

3.2.7. Geographic range

We estimated the latitudinal geographic range using paleolatitudinal data in the Paleobiology Database. We define latitudinal ranges as the differences between the northernmost and southernmost occurrences of each genus during the Pennsylvanian in the Paleobiology Database. A latitudinal range of 1 was defined for all genera with ranges smaller than 1 or for those general that lacked any occurrence in the Paleobiology Database.

3.2.8. Life habit

In order to study the effect of different life habits, we classified all genera in different guilds (Supplementary information). Guilds can account for differences in bauplans including taxonomic classification as a variable for their definition (e.g., Bambach, 1983). However, because we tested taxonomic identity separately, we did not use taxonomic classification for the definition of guilds. Hence, we defined two major guilds based on substrate usage, an epifaunal guild and an infaunal guild. All semi-infaunal taxa were classified as epifaunal (Thayer, 1979, 1983).

3.2.9. Selectivity

We used logistic regression to test selectivity in extirpation and immigration. Logistic regression is a generalized linear model that allows the analysis of the relationship between a binomial dependent (response) variable and a continuous or categorical independent (predictor) variable (Hosmer and Lemeshow, 2000). This method has the advantage of (1) being able to analyze either each variable alone or many variables together, and (2) compare the predictive power of each variable for explaining extirpation/immigration. Indeed, logistic regression has shown to be a very powerful method for analyzing selectivity (Payne and Finnegan, 2007; Clapham and Payne, 2011; Harnik et al., 2012; Payne et al., 2016).

The model is fitted by maximum likelihood, the overall fit of the model is measured with the Akaike information criteria (AIC, Burnham and Anderson, 2002) which is calculated as,

$$AIC = -2 \times \ln(L) + 2 \times K \tag{7}$$

where K is the number of parameters in the model and L is the likelihood of the model. Logistic regressions were fitted using the glm() function and stepwise selection was carried out with step() function in R (R Core Team, 2018).

Selectivity is measured by the log-odds ratio, which indicates the increase in the odds of extirpation/immigration as the value of the predictor variable increases in one unit (Hosmer and Lemeshow, 2000). Log-odds ratio of 0 indicates that there is no increment in the chance of extirpation/immigration as the predictor increases. A positive log-odds ratio indicates that the odds of extirpation/immigration increase, while a negative log-odds ratio indicates that the odds decrease as the value of predictor variable increases. Hence, the strength of the selectivity is measured by the absolute value of log-odds. The higher the absolute value, the stronger the selectivity. On the other hand, the nature of selectivity is measured by the log-odds sign (i.e. whether it is positive or negative), while log-odds close or equal to zero indicate lack of selectivity. Given the rational of our analysis negative extirpation log-odds indicate that extirpation was selective towards taxa with lower values of the given predictor, while positive log-odds to taxa with larger values. For instance, negative extirpation log-odds for geographic range indicate that extirpation was selective for taxa with smaller ranges. Similar logic is used for interpreting immigration selectivity. Negative log-odds indicate that immigration was selective for taxa with smaller values of a given predictor, while positive log-odds to taxa with larger values. Positive immigration log-odds for preferred depth (PD), for example, indicate that immigration was selective for taxa with higher preferred depth (PD). Taxonomic identity represents a particular case, because there are no larger or smaller values of the predictor variable. Hence, positive log-odds indicate selectivity for brachiopods and negative log-odds for bivalves.

To test whether log-odds ratios are significantly different from zero we used 95% confidence intervals based on the profiled log-likelihood function, which were calculated using confint() function in MASS package for R (Venables and Ripley, 2002). Therefore, if the range of the confidence interval includes zero, the given variable is non-significant for selectivity. This approach is analogous to significant testing at a level of $\alpha = 0.05$ (Lane, 2013). We define that a variable is marginally non-significant if the 95% confidence interval includes zero, but

the 90% confidence interval does not.

At a first step we fitted each individual variable for extirpation in the Bashkirian and immigration in the Moscovian-Kasimovian, and compared selectivity based on log-odds ratio confidence intervals. We then analyzed selectivity with a multiple logistic regression without interactions using all six predictors (i.e. taxonomy, preferred depth, environmental breadth, body size, metabolic rate and life habits), and selected the variable(s) that best explained the extirpation or immigration with a stepwise algorithm based on AIC (Anderson et al., 2000; Burnham and Anderson, 2002). AIC does not measure significance, but the fit of the regression model. Therefore, a selected variable could still be non-significant based on confidence intervals, but be relevant for the model because it increases the model's fit relative to model's complexity (i.e., number of explanatory variables).

At a second step, we analyzed extirpation and immigration within each environment separately. We performed this analysis in order to understand whether survival was driven by selectivity in one environment alone, or whether different environments recorded different selectivity dynamics.

At a third step, we studied brachiopods and bivalves separately both for extirpation and immigration. For each clade we fitted three response variables, namely preferred depth, environmental breadth and body size. We did not fit regional occupancy, nor metabolic rates, because maximum likelihood estimates were not possible due to quasi-complete separation.

For the ease of comparison of log-odds ratios of different predictors with variable magnitude ranges, we standardized all predictors previous to the analyses using the standardize method in decostand() function in vegan package for R (Oksanen et al., 2015).

3.2.10. Influence

Extinction and immigration log-odds are measures of selectivity that are independent of actual turnover intensity. Therefore, to study the combined effect of selectivity and intensity along the bathymetric gradient, we followed Payne et al. (2016) in using the concept of influence of extirpation and immigration. They defined influence as the geometric mean of the absolute value of log-odds and extirpation/immigration proportion.

For estimating extirpation/immigration we randomly subsampled 8 samples within each environment in each time bin. We then observed which of the present taxa did extirpate in the Bashkirian and immigrate in the Moscovian-Kasimovian. The procedure was repeated 1000 times to get the averages for extirpation and immigration.

4. Results

4.1. Extirpation selectivity

Logistic regression results highlight important differences in selectivity between predictor variables. At a first step we analyzed all variables independently. For most variables, namely occupancy, body size, metabolic rate, environmental breadth, preferred depth, life habit or geographic range, the log-odds confidence intervals contain zero, indicating that they are not significant. Therefore, none of these parameters predict survival across the glacial non-glacial transition (Fig. 4). Only taxonomic identity is a significant predictor of survival, as its confidence interval does not include zero. Positive log-odds indicate that bivalves preferentially survived while brachiopods were more prone to extirpation. The largest relevance of taxonomic identity among all single models is also supported by the lowest AIC value (Table 1).

The stepwise selection, however, indicates that the best model is a multivariate model including, in addition to taxonomic identity, geographic range and body size (Table 1). In this model, taxonomic identity is again the most important variable with significant log-odds and the highest absolute log-odds value. Positive log-odds indicate that brachiopods were significantly extirpated relative to bivalves (Fig. 4).
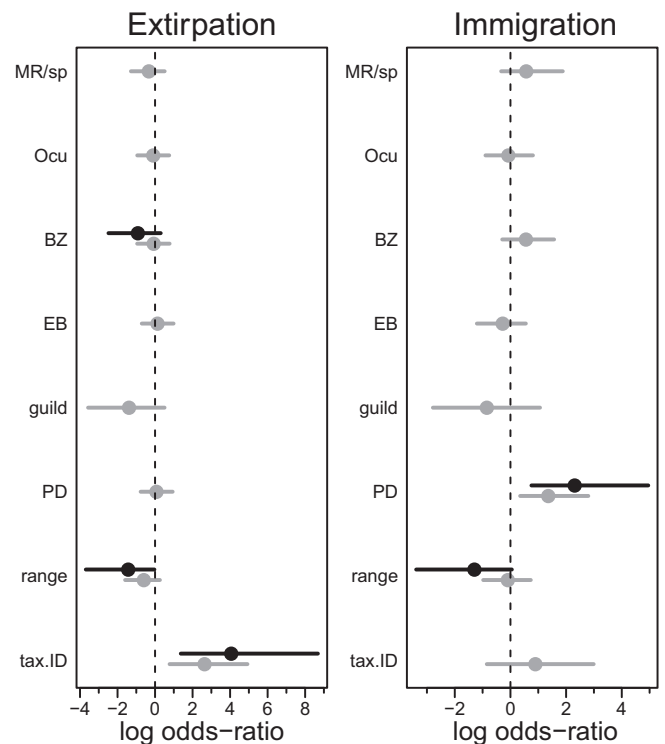

Fig. 4. Extirpation and immigration selectivity. Positive log-odds ratios indicate selectivity for taxa with larger values of a given trait. For taxonomic identity and guilds positive log-odds ratios indicate selectivity for brachiopods and epifaunal taxa respectively. In grey, log odds ratio for individual models. In black, log odds ratio for best multiple logistic regression. Dots are maximum likelihood estimates, error bars indicate 95% confidence intervals. **MR/sp**, Metabolic rate per genus; **Ocu**, occupancy; **BZ**, body size; **EB**, environmental breadth; **guilds**, life habit; **PD**, preferred depth; **range**, geographic range; **tax.ID**, taxonomic identity.

Table 1
Akaike Information Criteria for single and multiple models. Boldface indicates best models selected by the stepwise algorithm.

Parameter	AIC for extirpation selectivity	AIC for immigration selectivity
Taxonomic identity	28.55	36.57
Geographic range	34.76	37.49
Life habit	34.55	36.75
Preferred depth	36.57	30.02
Environmental breadth	36.51	37.12
Body size	36.57	35.94
Occupancy	36.55	37.51
Metabolic rate	35.99	36.13
Taxonomic identity + geographic range + body size	**27.77**	–
Preferred depth + geographic range	–	**28.51**

Geographic range also has significant log-odds. Negative log-odds indicate that taxa with small ranges were at higher risk of extirpation (Fig. 4). Negative log-odds for body size, also indicate that taxa with smaller body sizes were preferentially extirpated. Body size selectivity is not significant because confidence intervals include zero (Fig. 4). Nevertheless, the relevance of body size in extirpation selectivity is emphasized by the fact that it was selected as part of the best model.

Then we fitted the best model in each environment in order to study selectivity trends along the bathymetric gradient (Fig. 5). Brachiopods were selectively extirpated in all environments, as taxonomic identity exhibit similar positive log-odds values along the whole bathymetric
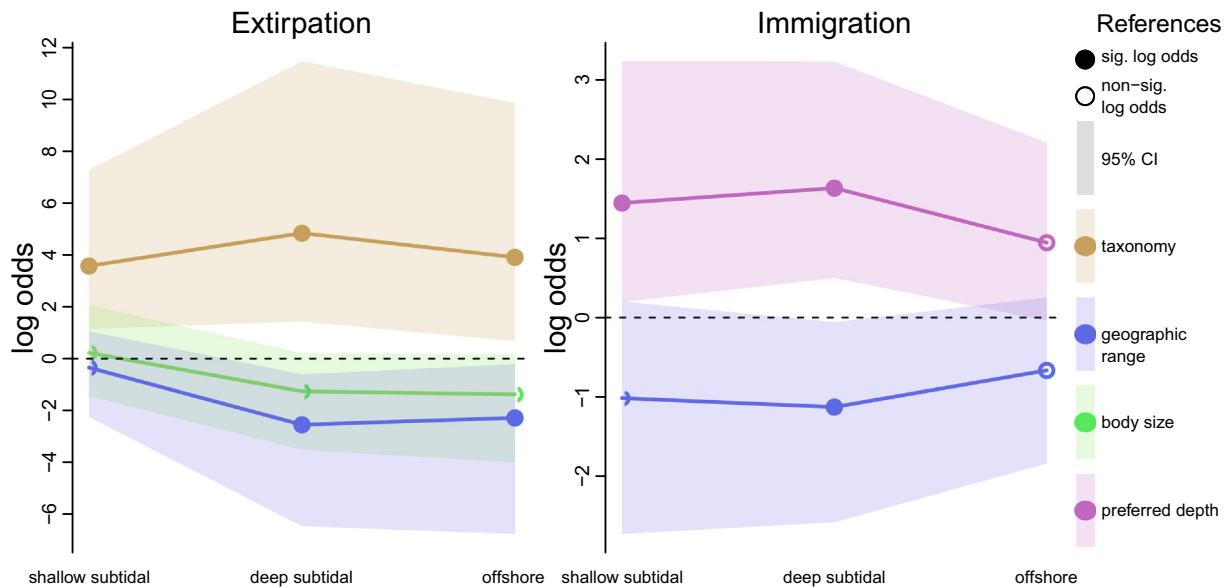
Fig. 5. Extirpation (left) and immigration (right) selectivity along the bathymetric gradient. Dots are maximum likelihood estimates, envelopes indicate 95% confidence intervals. Log odds ratios correspond to the best multiple logistic regressions based on the whole dataset. See Fig. 3 for further detail.

gradient. Hence, selectivity for brachiopods is significant, as log-odds confidence intervals do not include zero in any environment. Geographic range and body size, however, show a different environmental trend in selectivity (Fig. 5). Geographic range log-odds become increasingly more negative towards the offshore, marking an increase in the strength of geographic range selectivity towards deep environments. (Fig. 5). Such a pattern indicates that the deeper the environment, the stronger the extirpation selectivity for taxa with small geographical ranges. Moreover, in the shallow subtidal there is no significant selectivity at all, because the log-odds confidence interval in this environment includes zero. Both deep subtidal and offshore environments show significant extirpation selectivity. Body size selectivity shows a similar trend. Log-odds are increasingly more negative from shallow to deep environments, highlighting stronger selectivity for smaller sized taxa in deep environments. Log-odds for body size are not significant in any environments because confidence intervals always include zero (Fig. 5). However, log-odds in both the deep subtidal and the offshore are marginally non-significant.

Comparing brachiopods and bivalves underscores that both clades differed in survival selectivity. Bivalves show negative extirpation log-odds for body size, which indicates selectivity towards small sizes (Fig. 6). In other words, in bivalves, larger body sizes buffered against extirpation. All other studied variables in bivalves lack any relevance, as confidence intervals invariably include zero. Moreover, the stepwise

selection indicates that body size alone is the best predictor for bivalve extirpation, as it has the lowest AIC. On the other hand, brachiopods do not show any variable with significant log-odds, because all confidence intervals include zero (Fig. 6). However, the stepwise selection based on AIC shows that the best model includes geographic range as the only explanatory variable. Therefore, although all variables were non-significant, it does not mean that taxa were randomly extirpated. Negative log-odds for geographic range indicates that extirpation in brachiopods was selective for small range taxa.

4.2. Immigration selectivity

The analysis of each parameter individually shows that, using single models, immigration is only related to preferred depth. Preferred depth is the only variable with significant log-odds, as its confident interval does not include zero (Fig. 4). In addition, it has the lower AIC among single models (Table 1). Positive log-odds indicate that immigration was selective for taxa inhabiting deeper environments (higher PD values). None of the other variables had significant log-odds, because all confidence intervals include zero. This indicates no relevant selectivity among these variables. The stepwise selection shows that the best model involves two explanatory variables. Both preferred depth and geographic range are selected as relevant variables (Table 1). In this multiple model, preferred depth (PD) has significant positive log-odds,
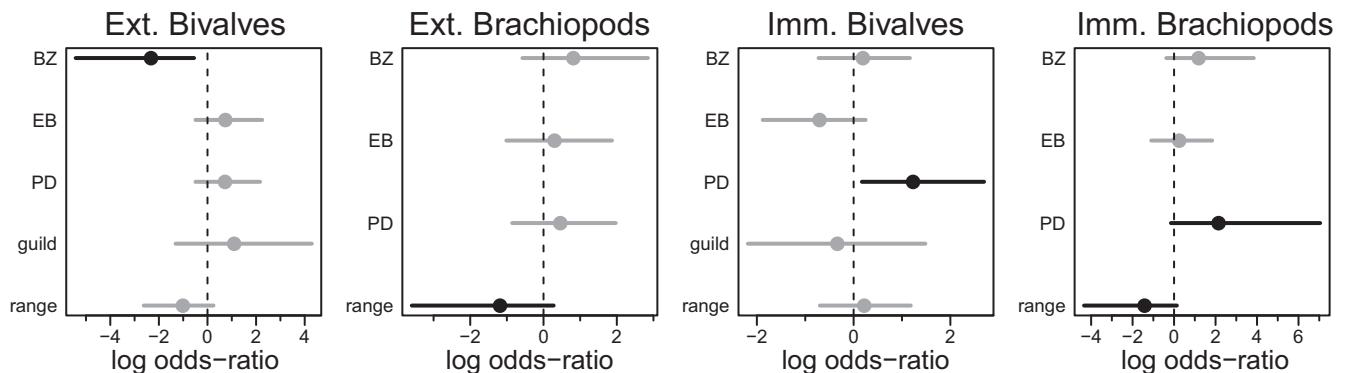

Fig. 6. Extirpation (left) and immigration (right) selectivity for bivalves and brachiopods. In black are log-odds ratios of the best model, other analyzed models in grey. Dots are maximum likelihood estimates, error bars indicate 95% confidence intervals. Imm., immigration; Ext., extirpation.

indicating that immigrants preferred deeper environments. Although geographic range was selected as part of the best explanatory model, log-odds are marginally non-significant. Negative log-odds for geographic range indicate that immigrants preferentially had smaller ranges. (Fig. 4).

When analyzing immigration along the bathymetric gradient, we can see positive log-odds for preferred depth (PD) in all three environments. Such a result underscores selectivity for taxa with preference for deeper environments all along the bathymetric gradient (Fig. 5). Log-odds confidence intervals for PD do not include zero in the shallow and deep subtidal, indicating significant selectivity in these environments. Nevertheless, selectivity decreased towards the offshore as log-odds for PD are lower and marginally non-significant in this environment. Selectivity based on geographic ranges is also high in the shallow and deep subtidal, decreasing towards the offshore (Fig. 5). Although shallow and deep subtidal have similar log-odds, significant selectivity is achieved only in the deep subtidal. The latter is the only environment where confidence intervals do not include zero (Fig. 5). Negative log-odds indicate selectivity for small geographic ranges in immigrant genera.

In bivalves, immigration is only related to preferred depth, because PD is the only variable with significant log-odds (Fig. 6). Moreover, the stepwise algorithm selects it as the only relevant variable (Table 2). Positive log-odds underscores that bivalve immigration was related to preference for deep environments. In brachiopods, however, immigration is both related to depth preference and geographic ranges (Fig. 6). Positive log-odds for PD indicates that brachiopod immigrants had preference for deep environments. Negative log-odds for geographic ranges on the other hand, indicates that brachiopod immigrants preferentially had small ranges. Both variables have marginally non-significant log-odds. Nearly identical AIC values for both variables suggest that both have almost equal explanatory power. (Table 2). Stepwise selection indicates that both geographic range and preferred depth are included in the best explanatory model (Table 2). Unfortunately, estimation of log-odds confidence intervals based on this multiple model is not possible due to insufficient data. Nevertheless, log-odds ratios did not change substantially between the best selected multiple model and those based on single models. Therefore Fig. 6D only shows log-odds based on single models.

4.3. Influence

The influence of extirpation follows a clear environmental trend with all three factors have higher influence in deeper environments. Environmental trend is steeper in geographic range and body size than in taxonomic identity. However, taxonomic identity shows the stronger influence on the biota as it has the highest values (Fig. 7). On the other hand, both geographic range and preferred depth show relatively high influence of immigration, but no environmental trend at all (Fig. 7).

5. Discussion

5.1. Extirpation selectivity

One main issue for the current analysis is whether any selectivity pattern observed could be just a regional expression of global selectivity, or an actual consequence of the climatic change witnessed in the region. There are some evidences that suggest that turnover in western Argentina is probably not mirroring global selectivity dynamics. First, Balseiro (2016a) showed that regional turnover in western Argentina was higher than Pennsylvanian global or tropical rates (Bonelli and Patzkowsky, 2008; Badyrka et al., 2013; Stanley and Powell, 2005). Second, most taxa extirpated in the region did actually survive elsewhere, suggesting that the driver of extirpation is necessarily regional rather than global.

Our results coincide with the widely accepted idea that clade membership has an important role in determining the survivorship of a given species (Smith and Roy, 2006). As shown by Balseiro (2016a) for this turnover event, bivalves show preferential survivorship, while brachiopods are strongly extirpated. It is very improbable that taxonomy itself was the actual factor underlying selectivity, but some biological trait or ecological characteristic that differs between most brachiopods and bivalves. For example, the impact of the Triassic-Jurassic extinction differed among taxonomic groups (classes or phyla) varying from strong in some taxa to nearly absent in others (Kiessling et al., 2007). The actual driver for this taxonomic selectivity was most probably habitat preference, where higher extinction rates were exhibited in reef and shallow environment dwellers (Kiessling et al., 2007). However, such an environmental sieve is unlikely to have been relevant across the glacial non-glacial transition in central western Argentina, because preferred depth is not relevant for extirpation nor when studied alone or together with taxonomic identity. Therefore, extirpated taxa and survivors do not differ in their preferred depth (Balseiro and Halpern, 2016).

Other possible explanation could be based on life habit, as all rhynchonelliform brachiopods are epifaunal while many bivalves are infaunal. Life habit has been suggested as major control for differential ecological patterns between brachiopods and bivalves (Bonuso and Bottjer, 2006). And it has shown to be relevant even within bivalves in the South American Pacific coast late Neogene extinction (Rivadeneira and Marquet, 2007) and the Toarcian (Lower Jurassic) extinction event (Aberhan and Baumiller, 2003). However, life habit did not buffer against extinction in our results.

Metabolic rates could also be important drivers of extinction (Strotz et al., 2018). Facing climate warming more active taxa (i.e. with higher basal metabolic rates) could preferentially survive as it has been shown in present-day biota (Peck et al., 2009) and past mass extinctions (Clapham, 2017). However, other analyses have shown that taxa with high metabolic rates could have higher risk of extinction (Strotz et al., 2018). In any case, such a scenario can be ruled out because our results show no selectivity based on metabolic rates. Our results agree with Clapham (2017) who found extinction selectivity related to organisms activity levels only in major mass extinction but no selectivity for

Table 2

Akaike Information Criteria for single and multiple models of brachiopods and bivalves separately. Best models in boldface are those selected by the stepwise algorithm.

| Parameter	AIC for extirpation selectivity in bivalves	AIC for extirpation selectivity in brachiopods	AIC for immigration selectivity in bivalves	AIC for immigration selectivity in brachiopods
Geographic range	18.32	**17.43**	31.3	15.42
Life habit	19.99	–	31.39	–
Preferred depth	19.41	19.37	**26.17**	15.39
Environmental breadth	19.34	19.64	29.48	18.42
Body size	**12.99**	18.63	31.95	16.5
Preferred depth + Geographic range	–	–	–	**9.95**
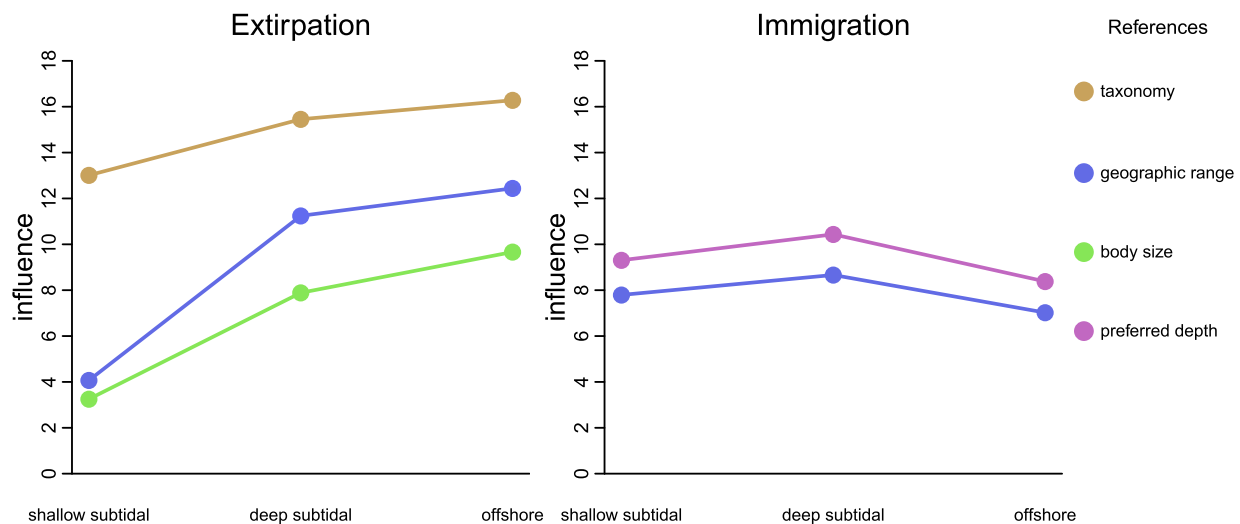
Fig. 7. Extirpation (left) and immigration (right) influence along the bathymetric gradient. See Fig. 3 for further detail.

background extinction. The lack of extirpation selectivity in western Argentina could indicate that the regional climatic event was not strong enough as to cause extirpation based on physiological aspects of the organisms.

In addition, two aspects of rarity (Rabinowitz, 1981), namely environmental breadth and occupancy, also lack any relevance in the analysis of extirpation risk in central western Argentina. While our result about the nonimportance of abundance (=occupancy) in extirpation risk agrees with previous global analyses (Harnik et al., 2012), the lack of relevance of environmental breadth contrast with such analyses (Harnik et al., 2012). The lack of selectivity based on environmental breadth has already been discussed by Balseiro and Halpern (2016). They conclude that it could be caused by the extinction at the beginning of the LPIA, which culled the marine fauna of stenoics taxa (Stanley and Powell, 2003; Powell, 2005).

Two factors have shown to be relevant for extirpation in central western Argentina, namely body size and geographic range. Both factors, however, are most probably not important for both clades because (1) both variables only arise as relevant when studied together with taxonomic identity, and (2) only bivalves show a strong selectivity for large body size survivorship, while brachiopods only show survival selectivity for large ranges. Therefore, differential extirpation of brachiopods and bivalves cannot be explained based on any studied biological characteristic. Indeed, brachiopods and bivalves differ in their mean background extinction rates during the late Paleozoic, with brachiopods having higher extinction rates (Stanley, 2007; Stanley and Powell, 2003). However, it is difficult to interpret the observed higher extirpation of brachiopods as an expression of global rates, because most extirpated genera did survive elsewhere (Cisterna, 2010).

It is not surprising that survival of bivalves was related to body size, because it is an important biological trait influencing extinction risk (Harnik, 2011). However, it is difficult to explain such a selectivity pattern in light of the temperature-size relationship (Sheridan and Bickford, 2011). It is expected that facing climate amelioration (i.e. warming), small taxa would show higher survivorship (Forster et al., 2012), as has been observed elsewhere in the fossil record (Finkel et al., 2005; Blois et al., 2008; Smith et al., 2009). However, an increase in mean temperature and an increase in temperature range, could have opposite responses in body size distributions (Gardner et al., 2011). While the first scenario would account for a reduction, the latter could cause an increase in body size. In fact, small sized taxa have shown selective disadvantages when briefly exposed to extreme temperature ranges during climate changes (Gardner et al., 2011 and references therein).According to these authors, water and energy balance in small

ectotherms can be severely affected due to their volume/area ratio. Mass die-offs records during heat waves evidence such limitation (Gardner et al., 2011). This suggests that the body size response to climate warming is not only influenced by the rate of temperature changes, but also by the extent of the thermal range. Thus, a possible scenario includes a rise in maximum temperatures, while minimum temperatures remained stable, setting the conditions for greater climate variability. Such a pattern of higher maximum values has also been identified during upper Paleozoic warm intervals in tropical regions (Powell et al., 2009). Therefore, the observed survival selectivity for bivalves with larger body sizes, might indicate that climate amelioration in marine environments of central western Argentina was more related to larger thermal amplitude.

Brachiopods, on the other hand, show selective extirpation for small geographic ranges. This result is not surprising, given that geographic range is the most important aspect of rarity related to extinction (Harnik et al., 2012). Large geographic ranges are related to survivorship because they buffer against environmental changes that occur in more restricted areas (Brown, 1995; Fritz et al., 2009; Harnik et al., 2012). Although such an explanation is useful for global analysis, it does not explain selectivity at regional scale (i.e., extirpations). Indeed, Powell (2008) found that latitudinal ranges explained extinction at global scale, but not extirpations, at the beginning of the LPIA in the Central Appalachian Basin. The observed extirpation selectivity in central western Argentina must, therefore, be responding to some characteristic related to large ranges, than to large ranges per se. Moreover, large geographic ranges have been related to tolerance for large temperature ranges outside the tropics (Gaston and Chown, 1999). Hence, extirpation in brachiopods could have been related to taxa with lesser tolerance for thermal amplitude.

Dispersal potential, however, could also explain the observed extirpation selectivity. Small range taxa are inferred to have lesser dispersal potential. The limited ability to disperse could explain why these taxa were not able to immigrate back to the basin during the Moscovian-Kasimovian transgression. And if a taxon did not immigrate back, it was necessarily extirpated. Although this possibility is very plausible, it does not explain why do body size and range size selectivity have the same environmental pattern (Fig. 5). If, on the other hand, extirpation selectivity in brachiopods was related to thermal amplitude, it would have been related, though in different fashion, to the same factor as extirpation in bivalves. In such a scenario, the similar environmental trend observed for selectivity for both body sizes and geographic ranges would not be surprising. The corresponding environmental pattern would reflect two possible strategies to face the

variations in thermal amplitude during an amelioration episode. Moreover, our results suggest that the impact of higher thermal amplitude was larger in deep waters. This result is counterintuitive, because larger thermal amplitudes are expected for shallow waters compared to deep ones (Lalli and Parsons, 2006). It is very possible, however, that during the glacial episode the mixed surface layer was restricted to environments above the storm wave base. But later, with the end of the glacial interval and subsequent warming of surface waters (González and Díaz Saravia, 2010; Sterren and Cisterna, 2010; Taboada, 2010), the thermocline position and mixed surface layer could have reached larger depths at least temporally. This would cause deep waters to have more variable temperatures than the previously stable cold waters.

5.2. Immigration selectivity

Marine faunal migration patterns have been inferred through major shifts in paleogeographic patterns (Clapham, 2010) and they are probably related to changes in temperature and oceanographic circulation that occurred as consequences of the LPIA (Montañez and Poulsen, 2013). In this context, the recognized immigration selectivity for deep environments and brachiopods with small ranges could shed light on the dynamics involved in the turnover across the glacial – non glacial transition. However, the affinity of immigrants for deep environments (Balseiro and Halpern, 2016) is puzzling in a context of immigration driven by climate amelioration (González and Díaz Saravia, 2010; Limarino et al., 2014). If immigrants arrived to the basin together with the introduction of warm waters (González and Díaz Saravia, 2010), it would be expected for them to have preference for shallow waters. However, as mentioned above, larger environmental changes were identified in deeper than shallower environments. Indeed, Balseiro (2016a) suggested higher productivity characterized deep environments during the Moscovian-Kasimovian. Therefore, immigrants could have preferentially settled in deeper habitats because of the amount of readily available resources, rather than having an actual preference for these environments. This possibility also explains why brachiopods and bivalves exhibit similar immigration preferences for deeper environments, despite both clades immigrated from different regions. If thermal preferences drove brachiopod and bivalve settlement, they would have most probably respectively established in deeper and shallower waters, because brachiopods immigrated from other high latitude Gondwanan or boreal basins (Cisterna, 2010) and bivalves came from low latitude Thethyan basins (Sterren, 2004).

On the other hand, the selective immigration of brachiopods with small geographic ranges is puzzling given that environmental change was also responsible for the extirpation of brachiopods with smaller ranges. One possible explanation for this selectivity pattern is that environmental conditions rapidly changed between the Late Serpukhovian-Bashkirian and Moscovian-Kasimovian faunas. A brief temporal lag between the two marine faunas is supported by the presence of a whole third order continental sequence recorded between the glacial and non-glacial marine transgressions across the basin (Limarino et al., 2006; Gulbranson et al., 2015). Moreover, rapid climatic differences during this interval are suggested by a transitional dynamic climate with short term ($< 10^6$ M) climatic fluctuations (Gulbranson et al., 2015) which took place at the end of the glacial episode, and before the settlement of stable arid conditions towards the Moscovian-Kasimovian (Gulbranson et al., 2015). All in all, evidence supports that climatic conditions differed between the end of the Bashkirian and the Moscovian-Kasimovian.

5.3. Environmental turnover gradients

In central western Argentina compositional turnover at the glacial non-glacial transition followed a clear environmental trend with higher turnover towards the offshore (Balseiro, 2016a). Moreover, Balseiro and Halpern (2016) showed that compositional turnover gradient was mostly driven by higher immigration in deep environments rather than extirpation. Therefore, it could be expected for selectivity in some traits to mirror the compositional turnover gradient. Any change in such traits should have also been related to larger influence of immigration in deeper environments rather than to extirpation.

Extirpation influence on body size and geographic range follows a clear trend along the bathymetric gradient (Fig. 7). Extirpation also records large influence on taxonomic identity, and although weaker, there is also an environmental signal with larger influence towards deeper environments (Fig. 7). Immigration influence on both preferred depth and geographic range, however, is intermediate in strength but stable along the bathymetric gradient. The difference in environmental trends of extirpation and immigration influence, suggests that the bathymetric gradient of body size, geographic ranges and brachiopod:bivalve proportion was remodeled by the turnover event. As previously mentioned, the influence of geographic range and body size did not have equal impact on brachiopods and bivalves. It is very probable that the remodeling of the bathymetric gradient in geographic range sizes was stronger in brachiopods, while in body size was stronger in bivalves.

Interestingly, the remodeling was in all three cases driven by the gradient in extirpation influence rather than immigration. This contrasts with the remodeling of the bathymetric diversity gradient that was driven by immigration (Balseiro, 2016a; Balseiro and Halpern, 2016). These results highlight that immigration and extirpation can be shaping different aspects of the bathymetric biotic gradient. Therefore, changes in body size or biogeographic structure in central western Argentina were not causally related to the increase in regional and local diversity (Balseiro, 2016a; Balseiro and Halpern, 2016).

6. Conclusions

The study of extirpation and immigration selectivity – using logistic regression – shed light on the dynamics underlying faunal turnover across a Pennsylvanian glacial to non-glacial transition in central western Argentina. In agreement with previous results, extirpation was shown to be stronger in brachiopods than bivalves. Moreover, both clades differed in their selectivity patterns. While brachiopods with smaller geographic ranges were selectively extirpated, bivalves with larger body sizes preferentially survived. This contrasting patterns, however, seem to respond to the same environmental change, namely larger thermal ranges. Immigration selectivity was not related to taxonomy but to the environmental preferences of immigrants. The preference of immigrants for deep environments suggests that their settlement was not controlled by thermal preferences but resource availability. Nevertheless, brachiopods immigrants did differ from bivalves in preferentially having smaller geographic ranges. The similarity between brachiopod extirpation and immigration selectivity suggests that (1) extirpation and immigration events were temporally separated and (2) rapid climatic changes occurred between the two faunas. Further analysis of selectivity along the environmental gradient indicates that extirpation selectivity probably remodeled the bathymetric gradients of geographic range size, body size and brachiopod:bivalve ratio. This contrasts with the modification of the diversity gradient, that was previously shown to be controlled by immigration rather than extirpation.

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Appendix A. Supplementary data

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